COMMON INACCURACIES IN FERTILITY PARAMETERS OF MATRIX POPULATION MODELS AND SUGGESTIONS FOR CORRECTIONS

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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December 2019

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Matrix population models are often applied to a variety of organisms possessing different life history traits, and fertility rates need to be estimated differently for them. Although there is a general method described for estimating fertility rates, there is a substantial variability in the ways fertility rates are estimated. The objective of this study was to evaluate the clarity and accuracy in estimating fertility parameters for their use in matrix population models with the intention of developing a transparent guide that would assist in overcoming the most frequent errors.

The study involves a meta-analysis of published articles that constructed a matrix population model for organisms within the Kingdom Animalia. Literature is organized into different animal group categories including, invertebrates, fish, birds, reptiles, and large mammals. Within each category each individual study is categorized based on whether it included sufficient information about estimating fertility rates and if the methods used for parameters were correct. In addition, results are compared with the corresponding life history traits of the organisms. Results indicate mistakes in estimating fertility occurred more frequently due to the omission of survival rate into the fertility coefficient and mistakes were also seen higher among opportunistic strategists and birth-pulse structured models. Of the studies sampled, mistakes in estimating fertility did not decrease over the ten year study period. These results suggests that perhaps mistakes continue to be present as a result of the entanglement between fecundity and fertility that has remained throughout literature.

A descriptive set of methods are developed to address the common mistakes found in the literature review. However, further development of tools to assist ecologists in applying matrix population models are needed.

DEDICATION

To my parents Carlos and Marialuisa Diaz for always offering their assistance in any form, for all of their sacrifices to ensure I had better opportunities than themselves, and for teaching me the value and importance of obtaining higher education. Thank you.

ACKNOWLEDGEMENTS

This project was funded in part by NSF OCE 1656923 to Masami Fujiwara. I would like to thank my committee chair, Dr. Fujiwara of the Department of Wildlife and Fisheries Sciences at Texas A&M University for his encouragement to pursue a higher education and his guidance throughout this process. I would also like to thank my committee members, Dr. Wang and Dr. Rogers for their support and guidance through the course of this research.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Dr. Masami Fujiwara (advisor) and Dr. Hsiao-Hsuan Wang of the Department of Wildlife and Fisheries Sciences and Dr. William E. Rogers of the Department of Ecosystem Sciences.

Funding Sources

Graduate study was supported in part by NSF OCE 1656923 to Masami Fujiwara.

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1. INTRODUCTION

Matrix population models are a useful tool for calculating population's growth rate (λ), stable stage distribution, reproductive value, generation time, and other related quantities (e.g. Caswell 2001). Information obtained from matrix population models, such as population growth rate and generation time, has been used for establishing the status of a potentially threatened species (Crouse et al. 1987; Beissinger & Westphal 1998; Musick 1999). The development of elasticity and sensitivity analysis has further allowed biologists to assess the relative contributions of different vital rates to λ (e.g. Caswell 2001; Crone et al. 2011; Morris & Doak 2002). These analyses are frequently used to guide wildlife management efforts (Manlik et al. 2017). With the rapid increase in the use of matrix models in population management, the misconstruction of these models has increased (Fujiwara & Diaz-Lopez, 2017; Kendall et al., 2019). Among these mistakes, errors while estimating reproductive parameters for a population are recurrent, as there is substantial variability in the way fertility rates are estimated across different taxa exhibiting different life histories. A fertility rate is given by the fecundity (number of offspring at their births per adult) times the survival rate of adult or offspring (Crowder et al., 1994; Fujiwara, 2007). However, the terms fertility and fecundity are often used interchangeably, or defined differently, in the literature leading to the use of a fecundity measure in a matrix without the incorporation of survival in the parameter. Without incorporating survival rate into the fertility parameter, there is a supposition that all offspring will survive to the following time step and this, in turn, will inflate λ.

Reproductive strategies of populations are generally categorized into birth-flow (Fig.1a) or birth-pulse populations although there are also many examples that exhibit intermediate strategies. A birth-flow population is one that is characterized by births occurring continuously

over the projected interval, and a birth-pulse population is characterized by birth occurring in a distinct reproductive season during the projection interval, which is the unit time interval over which a population is projected with a population matrix. Fertility associated with a birth-flow population is given by the weighted sum of fecundity where the weight is given by the survival of parents until reproduction and the survival of offspring over the remaining time during the projection interval (Caswell 2001). For example, the following equation can be used for approximating birth flow fertility rate of an age-structure matrix population model (Brault & Caswell, 1993):

$$F_i = l(0.5) * \frac{(m_i + P_i m_{i+1})}{2}$$

where fertility F_i is the product of the average number of births m_x in age class $x=i$ and the subsequent age class $x=i+1$ and the probability of an individual surviving to one-half of the projection interval $l(0.5)$. Where P_i denotes the survival rate for age class $x=i$ needed to reproduce at rate m_{i+1}.

In a birth-pulse population, births occur once within a seasonal period or year depending on the breeding patterns. The fertility rate is given by the product of adult survival until the reproductive season, fecundity, and the survival of offspring from the reproduction until the end of the projection interval. Matrix population models under a birth pulse model can be further categorized into a pre-breeding census (Fig.1b) or post-breeding census (Fig.1c) models when observations of a population occur immediately before reproductive season or immediately after reproductive season, respectively. The distinction between the two types is important for estimating fertility parameters. In a pre-breeding census model, fertility is calculated as the product of expected fecundity of *i*th age/stage class and the survival from birth to age *one*. In a post-breeding census model, fertility is the product of fecundity of *i*th age/stage class and

probability of survival of parents (*i*th age/stage class) over the projection interval (Cooch et al. 2002).

$$\text{Pre-breeding census}: F_i = l(1)m_i$$

$$\text{Post-breeding census}: F_i = P_i m_i$$

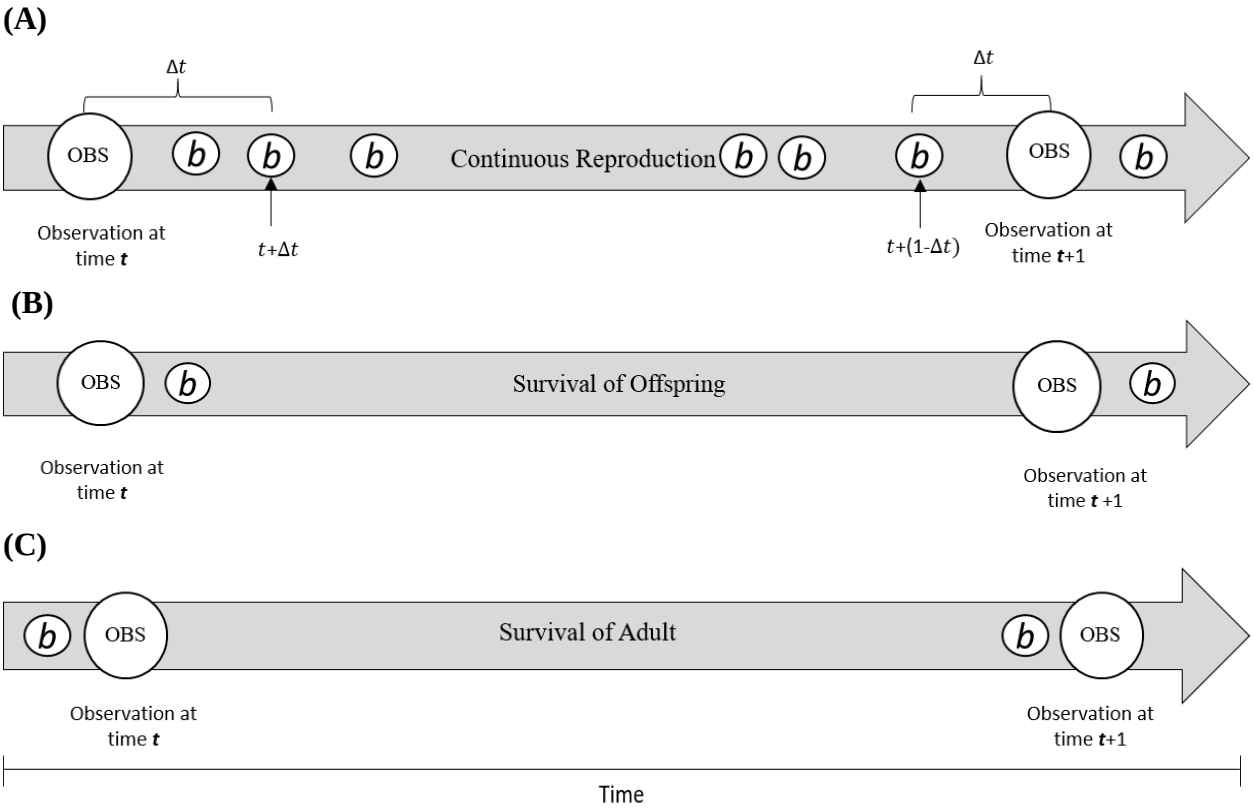

Figure 1. Graphic representation of (A) birth-flow populations, where reproduction (b) can occur continuously between observations (OBS) at time t and t+1, (B) birth-pulse population with a post-breeding census where reproduction occurs before time t of observation, (C) birth-pulse population with a pre-breeding census where reproduction occurs after observation at time t. Projection interval here is one year, however it may vary in other censuses.

A common mistake in modeling birth-pulse populations is using the wrong survival probabilities for the fertility calculation. This mistake will affect the fertility value used to

parameterize the matrix model, which can lead to a notable difference in population growth rate. This difference in population growth rate is especially noticeable if there is a large difference between immature and mature age class survival rates.

Errors in fertility estimation can also occur when reproduction occurs somewhere in the middle of the projection interval, and survival rate is not corrected for the probability of surviving for the fraction of a time unit. Finally, failing to incorporate the probability of individuals surviving over the time interval into the fertility rate can also affect the results of the matrix population model analysis. When evaluating the impacts of failing to include survival probability into the fertility coefficient, Kendall et al. (2019) concluded the asymptotic population growth rate was always overestimated. In addition, adult stable stage distribution, and adult reproductive value were also affected.

This thesis begins with a literature review. To gauge the current status of user errors, recent studies published in the last ten years (2007-2017) administering matrix population models are evaluated on their clarity in describing fertility parameters as well as their accuracy in correctly inputting it into the matrix. The aim of this study is to conduct a meta-analysis of published literature using Web of Science with specific keywords such as "Matrix Population Model" and group them based on taxa and different life history traits as defined by Winemiller & Rose (1992). The three life history strategies are opportunistic, equilibrium, and periodic. Where opportunistic strategists are characterized by relatively high fecundity, low juvenile survival rate, and low adult survival rate. Equilibrium strategists are characterized by relatively low fecundity, high juvenile survival rate, and high adult survival rate. Periodic strategists are characterized by relatively high fecundity, high juvenile survival rate, and high adult survival rate. Due to the complexity of plant reproductive strategies, matrix population models pertaining to species within the Kingdom

Animalia are the focus of this study. Once species are grouped into different taxa and life history traits, the articles are examined regarding the correctness of fertility parameters using a list of criteria, with special attention to time scale. In doing so, trends in errors are to be determined among different life history traits as well as different taxa. The goal of this literature review is to address prevalent mistakes and discuss how to overcome these caveats.

After the literature review, methods used for the corrections of an alligator matrix population model (Dunham et al., 2014), which happened to omit survival rate in the original paper, are described in detail. The alligator matrix is one of the two matrices provided in Appendix A of Kendall et al. (2019), as part of a collaboration. After presenting the results of the literature review and the methods used with the alligator matrix, the thesis is concluded by presenting a set of protocols that can be used to avoid mistakes when estimating fertility rate for populations that exhibit birth-pulse reproductive strategies. These protocols are developed given the common mistakes found through the literature review. These protocols are aimed to assist ecologists that have suitable data for the construction of matrix population models but are inexperienced in configuring fertility rate that will correctly represent the population of interest.

2. METHODS*

2.1 Literature Review

A search in the Web of Science database was performed in January of 2018. Papers containing the terms "Matrix Population Model", "Lefkovitch Matrix Model", or "Leslie Matrix Model" in the title or abstract between the years 2007-2017 were identified. Studies published in theoretical modeling-based journals were not considered for review, and only species within the animal kingdom were considered. The studies were first reviewed to see if sufficient information regarding the estimation of fertility was provided. The information was considered sufficient when the following information was included: (i) clear description of method used to measure fertility, (ii) clear description of the way data were converted into fertility rate or actual equations used, and (iii) parameterized matrix was provided or detailed description of how parameters were input into the matrix allowing for replication (Fig. 2). This information was searched within a paper, its appendix, and any references cited in a method section.

The studies that were considered to have sufficient information were then organized into five main categories representing the taxa: invertebrates, fish, birds, reptiles, and mammals. Then, they were categorized based on life history strategies. To assign a life history strategy, the fecundity, juvenile survival, and time-interval used for matrix population model in the paper were considered. The time-interval between each projection of the model was used as an indication of generation time. Assigning a particular amount of time to be considered small generation time and large generation time to all taxa became challenging, and individuals were considered to have small generation time only when such time-intervals were small. Models with time-steps that were small (less than six months) were only used for short-lived species. Individuals were considered to have long generation time when supporting information was given on this particular trait.

*Part of this section is reprinted with permission from "Persistent Problems in the Construction of Matrix Population Models" by Kendall, B. E., Fujiwara, M., Diaz-Lopez, J., Schneider, S., Voigt, J., & Wiesner, S., 2019. *Ecological Modelling, 406*, 33-43, Copyright 2019 by Elsevier B.V.

Establishing long generation time varied among the different taxa groups, and populations that showed a generation time well above what could be considered typical for similar species were considered to have long generation time.

Fecundity was assessed by comparing individual fecundity to what may be considered typical for individuals in other populations within the same taxonomic class rank. High fecundity was assigned to invertebrates and fish, which had well over a hundred eggs per iteration. According to NestWatch source from The Cornell Lab of Ornithology (*Cornell Lab of Ornithology,* 2019 Cornell University), most common birds have clutches that range anywhere from 2-6 eggs per clutch. For this reason, high fecundity was assigned to populations in which individuals had seven or more eggs per clutch. Due to large variation within the reptile and mammal groups, fecundity was assessed using more literature-based interpretation of individuals' life history. Thus, high fecundity was assigned to populations that had supporting literature noting this life history trait.
Life history strategy was not assigned to papers when a matrix population model was used for multiple species as strategies would vary within study depending on species. Opportunistic strategies were assigned to populations consisting of individuals with low fecundity, low juvenile survival rate (<0.5), and a short generation time (time-step<6 months). Periodic strategies were assigned to populations consisting of individuals with high fecundity, low juvenile survival rate (<0.5), and long generation time. Equilibrium strategists were assigned to populations with individuals with low fecundity but high juvenile survival rates (≥0.6). When the paper being reviewed did not include one or more rates, externally published sources for same species or closely related species were used. Populations that did not fit the characteristics of these three strategies were considered to be intermediate strategists.

Finally, each study was assessed to determine if it appropriately implemented fertility rate into a population matrix. It was considered appropriate when the fertility rate was calculated using previously established fertility functions adjusting for birth-flow and birth-pulse reproductive patterns as well as age-classified and stage-classified models (Caswell, 2001). For stage-classified models, fertility estimated using a post-breeding census must have also included transition probabilities between stages (Caswell, 2001). More specifically, the fertility coefficient was assessed to determine if it included (a) fecundity in terms of offspring per parent or female offspring per female (female dominant assumption) and (b) survival rate of parent and/or offspring, encompassing the full-time interval of the model. Additional to (a), if the fecundity term was expressed in offspring per parent, the sex ratio must be included to account for the female offspring that will later contribute to the reproduction of offspring. Often the sex ratio is said to 0.5, for the probability of offspring being a female. However, if the population exhibits consistent differences between the ratio of females and males that make up the population, the ratio of population that is female should be used. Additional to (b), in a scenario where multiple survival rates were present to account for developmental changes occurring within a time step, then the survival rates must reflect the fraction of the time step for which the survival rate was measured. Steps used to determine the validity of the fertility coefficient are illustrated in Figure 2.

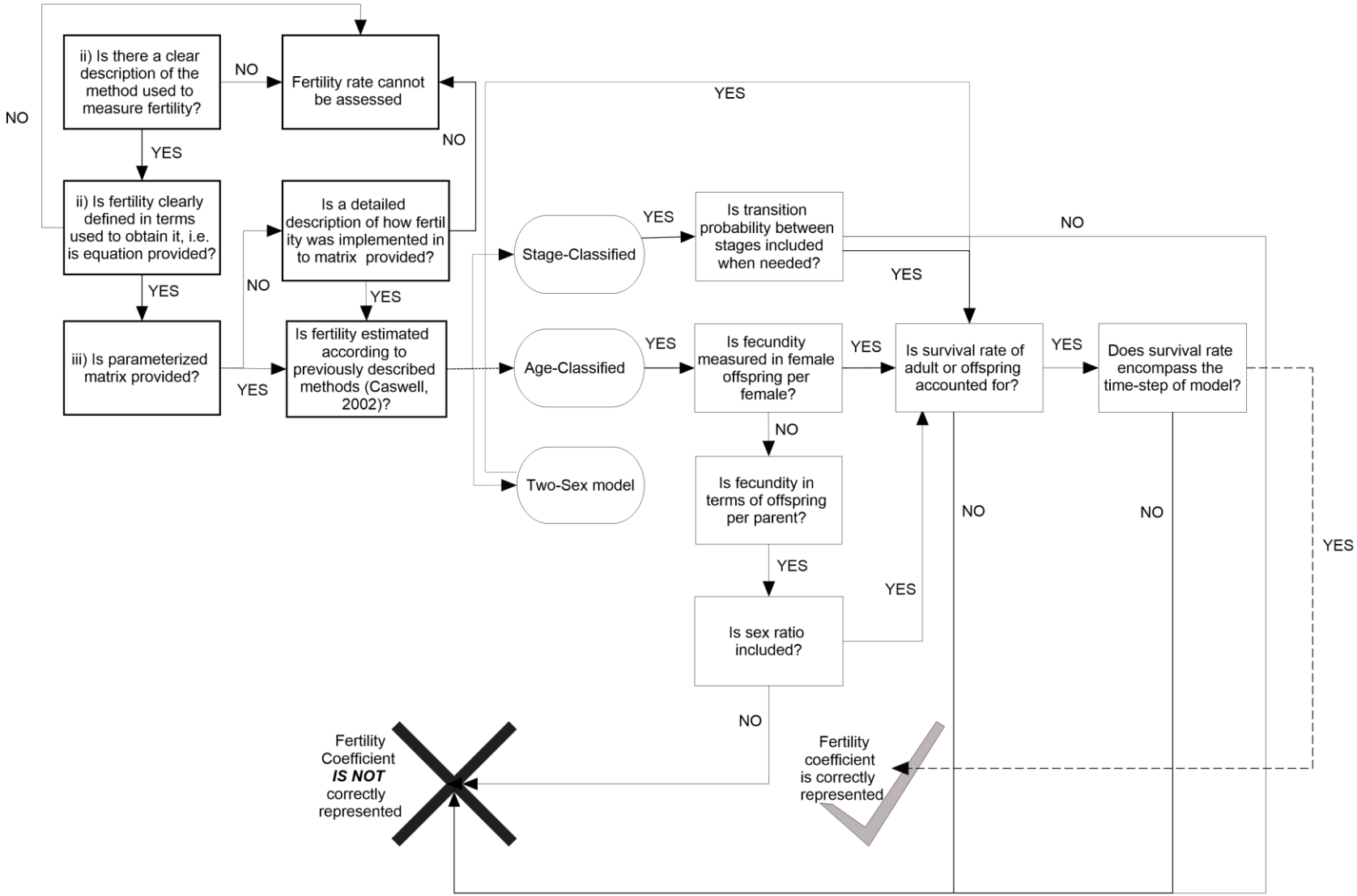

Figure 2. Decision tree used to identify literature eligible for review and steps used to evaluate the validity of the fertility coefficient used in the matrix population model.

2.2 Construction of American Alligator Matrix Population Models

The construction and reconstruction of a matrix population model was carried out for a study that was surveyed as part of the literature review. These methods and analysis were performed as part of a collaboration in the paper titled *Persistent Problems in The Construction of Matrix Population Models* (Kendall et al., 2019), and are also provided in the Appendix of this publication.

Stage-structured population matrices were constructed for two alligator populations by Dunham *et al*. (2014) to compare the status of northern and southern populations. Dunham *et al*. (2014) took parameters from other studies (Table 1), and constructed a model consisting of five stages for each population. The study used the same rates for both populations due to the lack of population specific estimates of survival rates.

Table 1. Parameter values for northern and southern populations of Alligator. These values are used for our calculations. Modified from Dunham et al. (2014)

Stage: i	***Size (cm)***	***Stage Duration*** D_i ***(years)***	***Survival Rate*** S_i	***Fecundity f (number x year^{-1})***
Northern Population				
Egg: E	*0*	*0.25*	*0.54* ***(per 3 month)***	*0.00*
Hatchling: H	*<30*	*1.00*	*0.38* ***(year^{-1})***	*0.00*
Juvenile: J	*30-121*	*7.00*	*0.78* ***(year^{-1})***	*0.00*
Subadult: S	*122-182*	*7.00*	*0.73* ***(year^{-1})***	*0.00*
Adult: A	*>183*	*>30.00*	*0.83* ***(year^{-1})***	*2.37*
Southern Population				
Egg: E	*0*	*0.25*	*0.54* ***(per 3 month)***	*0.00*
Hatchling: H	*<30*	*1.00*	*0.38* ***(year^{-1})***	*0.00*
Juvenile: J	*30-121*	*3.00*	*0.78* ***(year^{-1})***	*0.00*
Subadult: S	*122-182*	*3.00**	*0.73* ***(year^{-1})***	*0.00*
Adult: A	*>183*	*>30.00*	*0.83* ***(year^{-1})***	*5.98*

* Dunham et al. (2014) shows four years as the duration for subadult. However, we needed to change the duration to three years to make the results consistent with those presented in the paper.

Further details about the matrix models were not provided except that the Crouse *et al.* (1987) method for calculating the retention rate and transition rate in a stage-structured model was used. We constructed two matrices, one for each population to represent the original matrices described in the paper. The matrix models in Dunham *et al*. (2014) were five-stage models (*E*: egg; *H*: hatchling; *J*: juvenile; *S*: subadult; and *A*: adult) where a population matrix is given as:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & R_A \\ G_E & 0 & 0 & 0 & 0 \\ 0 & G_H & P_J & 0 & 0 \\ 0 & 0 & G_J & P_S & 0 \\ 0 & 0 & 0 & G_S & P_A \end{pmatrix}.$$

The notation used to parameterize the matrix population model is summarized in Table 2. The values for these elements are shown in Table 3. We refer to the original matrices for northern and southern populations as AN1 and AS1, respectively (Table 4).

Table 2. Definitions of notation used for Alligator Matrix Model

Notation	
P_J	Probability of surviving and remaining in the ***juvenile*** stage
G_J	Probability of surviving and moving to the next stage (***subadult*** stage)
P_S	Probability of surviving and remaining in the ***subadult*** stage
G_S	Probability of surviving and moving to the next stage (***adult*** stage)
P_A	Probability of surviving and remaining in the ***adult*** stage
R_S	Fertility rate for ***subadult*** stage
R_A	Fertility rate for ***adult*** stage

Table 3. Elements of matrix population models for northern and southern alligator populations. Values are rounded values. To obtain exact values used in calculations, insert the parameter values in Table 1 into the notations shown in this table. Reprinted with permission from Kendall et al. (2019).

	North	South	Notation	North	South	Notation	North	South	Notation
Model	**AN1**	**AS1**	**AN1 & AS1**	**AS2**	**AS2**	**AN2 & AS2**	**AN3**	**AS3**	**A3N & AS3**
G_E	0.54	0.54	s_E	--	--	--	--	--	--
G_H	0.38	0.38	s_H	0.38	0.38	s_H	0.38	0.38	s_H
P_J	0.73	0.58	$\frac{\sum_{k=0}^{D_H-2} s_H^k}{\sum_{k=0}^{D_H-1} s_H^k} s_H$	0.73	0.58	$\frac{\sum_{k=0}^{D_H-2} s_H^k}{\sum_{k=0}^{D_H-1} s_H^k} s_H$	0.71	0.59	$\frac{\sum_{k=0}^{D_H-2} \left(s_H/\lambda\right)^k}{\sum_{k=0}^{D_H-1} \left(s_H/\lambda\right)^k} s_H$
G_J	0.047	0.20	$\frac{s_H^{D_H-1}}{\sum_{k=0}^{D_H-1} s_J^k} s_H$	0.047	0.20	$\frac{s_H^{D_H-1}}{\sum_{k=0}^{D_H-1} s_J^k} s_H$	0.074	0.19	$\frac{\left(s_H/\lambda\right)^{D_H-1}}{\sum_{k=0}^{D_H-1} \left(s_H/\lambda\right)^k} s_H$
P_S	0.70	0.56	$\frac{\sum_{k=0}^{D_H-2} s_S^k}{\sum_{k=0}^{D_H-1} s_S^k} s_S$	0.70	0.56	$\frac{\sum_{k=0}^{D_H-2} s_S^k}{\sum_{k=0}^{D_H-1} s_S^k} s_S$	0.68	0.56	$\frac{\sum_{k=0}^{D_S-2} \left(s_S/\lambda\right)^k}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} S_S$
G_S	0.034	0.17	$\frac{s_S^{D_S-1}}{\sum_{k=0}^{D_S-1} s_S^k} s_S$	0.034	0.17	$\frac{s_S^{D_S-1}}{\sum_{k=0}^{D_S-1} s_S^k} s_S$	0.054	0.17	$\frac{\left(s_S/\lambda\right)^{D_S-1}}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} s_S$
P_A	0.83	0.83	s_A	0.83	0.83	s_A	0.83	0.83	s_A
R_S	0	0	0	0.046	0.600	$\frac{s_S^6}{\sum_{k=0}^{6} s_S^k} s_S^{9/12} f s_E$	0.075	0.579	$\frac{\left(s_S/\lambda\right)^{D_S-1}}{\sum_{k=0}^{D_S-1} \left(s_S/\lambda\right)^k} s_S^{9/12} f s_E$
R_A	2.37	5.98	f	1.11	2.81	$s_A^{9/12} f s_E$	1.11	2.81	$s_A^{9/12} f s_E$

Table 4. List of models for American alligators and description of changes made to the original models. Reprinted with permission from Kendall et al. (2019).

Model		Description
Northern Population	**Southern Population**	
AN1	**AS1**	• Original five-stage model in Dunham et al. (2014)
AN2	**AS2**	• Four-stage model (hatchling, juvenile, subadult, and adult) • Incorporation of survival rate into fertility rate of adult stage • Addition of fertility rate to subadult stage
AN3	**AS3**	• Four-stage model • All of the corrections made in A2 • Calculation of juvenile transition rates using AAS model
AN4	**AS4**	• Age-structured model • Without survival of adults in fertility coefficient (i.e. original fertility coefficient) • With fertility on the last subadult stage
AN5	**AS5**	• Age-structured model • With survival of adults in fertility coefficient • Without fertility on the last subadult stage (i.e. the <1,12> element is 0
AN6	**AS6**	• Age-structured model • With survival of adults in fertility coefficient • With fertility on the last subadult stage

One of the major problems in the construction of the matrices was that, although the models assumed a post-breeding census, the fecundity term implemented into the matrix did not include adult or egg survival. To correct for this, we reduced the number of stages from five to four so that the first stage is hatchling, and the fertility rate was modified to include the survival rates of the egg (S_E) over three months and adult (S_A) over 9 months as $R_A = s_A^{9/12} f s_E$ where f is the product of mean clutch size, sex ratio, and percent of females breeding as defined by Dunham *et al.*. A visual representation for how adult and egg survival rates were both used in fertility is illustrated in Figure 3.

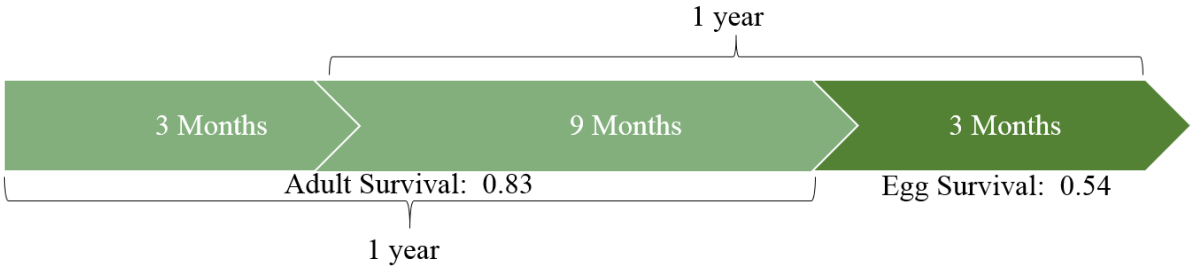

Figure 3. Arrow diagram representing time units used to measure Adult and Egg survival.

In addition, we also incorporated the fertility rate for the subadult stage as

$$R_S = \frac{s_S^6}{\sum_{k=0}^{6} s_S^k} s_S^{9/12} f s_E$$

where the first component of the equation shown as a fraction represents the transition rate from the subadult and adult stage. This transition rate is referred to as the stationary age-within-stage structure (SAS) model in Kendall et al. (2019), and assumes λ=1. To obtain it, the individuals

that survived the duration of the stage minus 1 (top half) is divided by the total number of individuals that were present at the beginning of the stage (bottom half). The equation is simplified so that survival rate and stage duration are needed as shown above for R_S.

Incorporating the fertility rate for the subadult stage, we assumed that individuals remain in the juvenile stage for seven years on average, but when they transition into adult stage, they also reproduce. A resulting population matrix is given as

$$\begin{pmatrix} 0 & 0 & R_S & R_A \\ G_H & P_J & 0 & 0 \\ 0 & G_J & P_S & 0 \\ 0 & 0 & G_S & P_A \end{pmatrix}.$$

In this matrix, other elements (i.e. *P*'s and *G*'s) remain the same except their locations in the matrix were changed as shown in the matrix above. We refer the modified matrices for the northern and southern populations as AN2 and AS2, respectively.

The method of Crouse *et al.* (1987) assumes that population growth rate λ to be 1. When the growth rate is far from 1, the survival rate in the transition calculation needs to be discounted with λ. This is because changes in λ affect the age distribution within a stage and hence the proportion of individuals maturing and transitioning to a new stage. Incorporating λ into the model is done by taking an initial guess, followed by the estimation of the fraction of individuals out of the stage *i* and dominant eigenvalue of the resulting matrix. The eigenvalue is then used as the new value for λ and the same method is repeated until the value of λ stops changing. The model with λ incorporated into the transition calculations (which affect P_J, G_J, P_S, G_S, and R_S) are referred as AN3 and AS3 for northern and southern populations, respectively. Where AAS is the asymptotic age-within-stage-structure model (Kendall et al. 2019) that uses transition rates discounted with λ as previously mentioned.

Finally, three Leslie matrices were constructed for northern and southern populations using the same survival rate as the stage-structured models. The Leslie matrices for the northern population (AN4-AN6) consists of 16 age classes, and that for southern population (AS4-AS6) consists of eight age classes. Under models AN4 and AS4, the parent survival rate was omitted in fertility rate so that adult stage and the last age class of subadult stage have positive fertility rate $R_i = s_i^{9/12} f s_E$ where i denotes the age class of parents reproducing. Under models AN5 and AS5, the fertility rate of the last age class of subadult was omitted so that only the last age class has fertility rate $R_i = s_i^{9/12} f s_E$. Finally, under models AN6 and AS6, both adult stage and the last age class of subadult stage have fertility rate $R_i = s_i^{9/12} f s_E$.

In total, twelve models were constructed with AN1-AN6 corresponding to the northern population and AS1-AS6 corresponding to the southern population. Elements of the population matrices for the six stage-structured populations are shown in Table 1.

Using the twelve population matrices, asymptotic population growth rate λ (Fig.6), stable stage distribution (Fig.7), reproductive value (Fig.8), the sensitivity (Fig.9) and elasticity (Fig.10) of the population growth rate to stage specific survival rate and fecundity (*f*), damping ratio (Fig.11), and generation time (Fig.12) were calculated. To obtain λ under AN3 and AS3 using the iterative method, initial λ was set to 1. Reproductive values for all models were scaled so that the reproductive value of the hatchling stage is 1. For calculating the stable stage distribution and sensitivity under AN4-AN6 and AS4-AS6 for the hatchling and subadult stages, corresponding values for age-classes were summed. Similarly, reproductive values for these stages under AN4-AN6 and AS4-AS6 were calculated by taking the weighted mean of reproductive values for corresponding age classes, where the weight is given by their stable stage

distribution. For calculating the sensitivity of lambda under all stage-structured models (i.e. except AN4-AN6 and AS4-AS6), numerical differentiation was used because juvenile survival S_J appears in multiple elements of these matrices, and λ appears in multiple elements under AN3 and AS3. The damping ratio measures how quickly transient dynamics dissipate over time and is given by the eigenvalue of the largest magnitude divided by the absolute value of the second largest eigenvalue (Caswell 2001). In this study, generation time was defined as the mean age of mothers and calculated using the formula in Bienvenu and Legendre (2015).

3. RESULTS*

3.1 Results for Literature Review

A total of 232 published papers were identified between the years 2007-2017 containing the terms “Matrix Population Model”, “Lefkovitch Matrix Model”, or “Leslie Matrix Model” in the title or abstract. The journal articles identified in this search are summarized in Table 5 with the frequency in which a paper used in the literature review belonged to said journal. The journals that were not considered in this review due to their tendency to focus more on theoretical framework rather than applied use of matrix population models are also tabulated. However, only 51 relevant studies were found to provide sufficient information and were further assessed. Of these 51 studies, 15 applied matrix population models on a species within the bird taxa, 13 on species within mammal taxa, 11 on invertebrate species, 9 on species within the fish taxa, and 3 on reptilian species.

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Table 5. List of journals corresponding to the 51 papers assessed where frequency indicates number of papers published within the obtained sample. Theoretical journals omitted from consideration of the resulting 232 papers are also listed.

Journal	Frequency	Omitted Journals
Aquaculture	1	*Journal of Mathematical Biology*
Aquatic Toxicology	1	*Journal of Theoretical Biology*
Biological Conservation	3	*Mathematical and Computer Modelling*
Canadian Journal of Fisheries and Aquatic Sciences	1	*Theoretical Ecology*
Chelonian Conservation and Biology	1	
Conservation Biology	1	
Ecological Modelling	3	
Ecological Monographs	1	
Ecology	2	
Endangered Species Research	1	
Environmental Toxicology and Chemistry	1	
Fisheries Research	1	
Functional Ecology	2	
Human and Ecological Risk Assessment: An International Journal	1	
Ibis	1	
Journal of Animal Ecology	1	
Journal of Applied Ecology	2	
Journal of Avian Biology	1	
Journal of Mammalogy	2	
Journal of Mathematical Biological	1	
Journal of Wildlife Management	5	
Marine and Freshwater Research	1	
Marine Ecology Progress Series	1	
Mathematical Biosciences & Engineering	2	
Molecular Ecology	1	
Natural Resource Modeling	1	
Neotropical Entomology	1	
PLoS One	3	
Population ecology	4	
Restoration Ecology	1	
Reviews in Fish Biology and Fisheries	1	
Scientific Reports	2	

The life histories consisted of a 22 equilibrium, 11 opportunistic, 10 intermediate, and 4 periodic strategists. Of the 51 studies, there were five papers that compiled data for multiple species. Due to life history strategies varying among species within a sole paper, strategies were not assigned to these papers. When examining the implementation of fertility rate into the matrix population models using previously established requirements, 26 out of the 51 papers failed to correctly estimate fertility rate. Among the different life history strategies assigned, papers having an equilibrium strategist had the highest number of papers marked as incorrect for the estimation of fertility. However, when looking at the proportion of incorrect papers, 31% of the papers with an equilibrium strategist were found to have an incorrect estimation of fertility, 55 % of opportunistic strategists, 66% of intermediate strategist, and 50% of periodic strategists (Fig. 4).

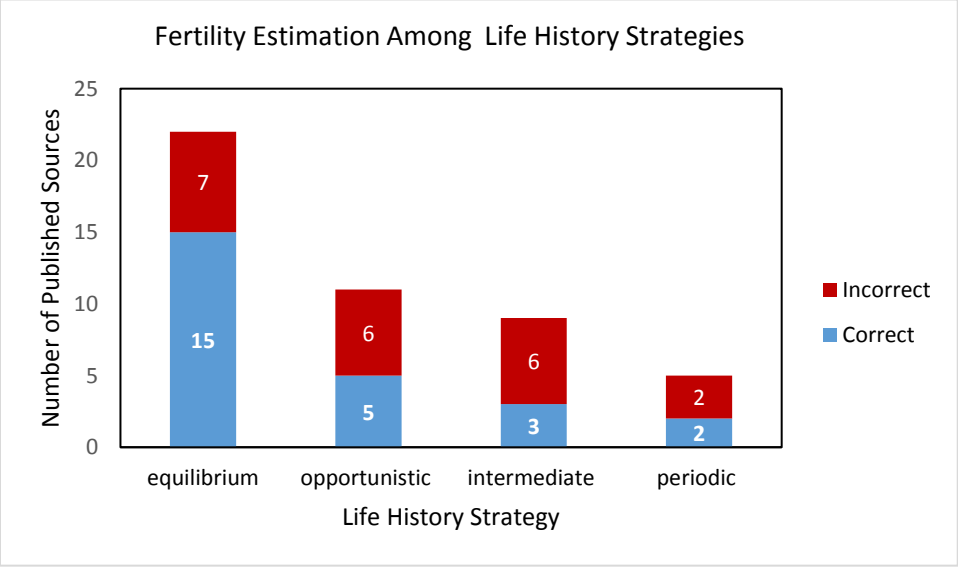


Figure 4. Bar graph illustrating proportion of correct vs incorrect estimation for fertility among different life history strategies.

When assessing fertility among the different taxa groups, 62% of papers grouped into the invertebrate taxa had incorrect estimation of fertility, 13% within fish taxa, 53% within bird taxa, 66% within reptile taxa, and 38% within the mammal taxa group (Fig.5). It is important to note the difference in sample size for each group. For instance, the reptile taxa group was underrepresented with a sample size of six papers of which only three were assessed. Among the papers failing to properly implement fertility into the matrix model, disregarding either adult or offspring survival was the most prevalent mistake. Additionally, of the 51 papers in this study, 36 assumed a birth-pulse model with either a post-breeding or pre-breeding census.

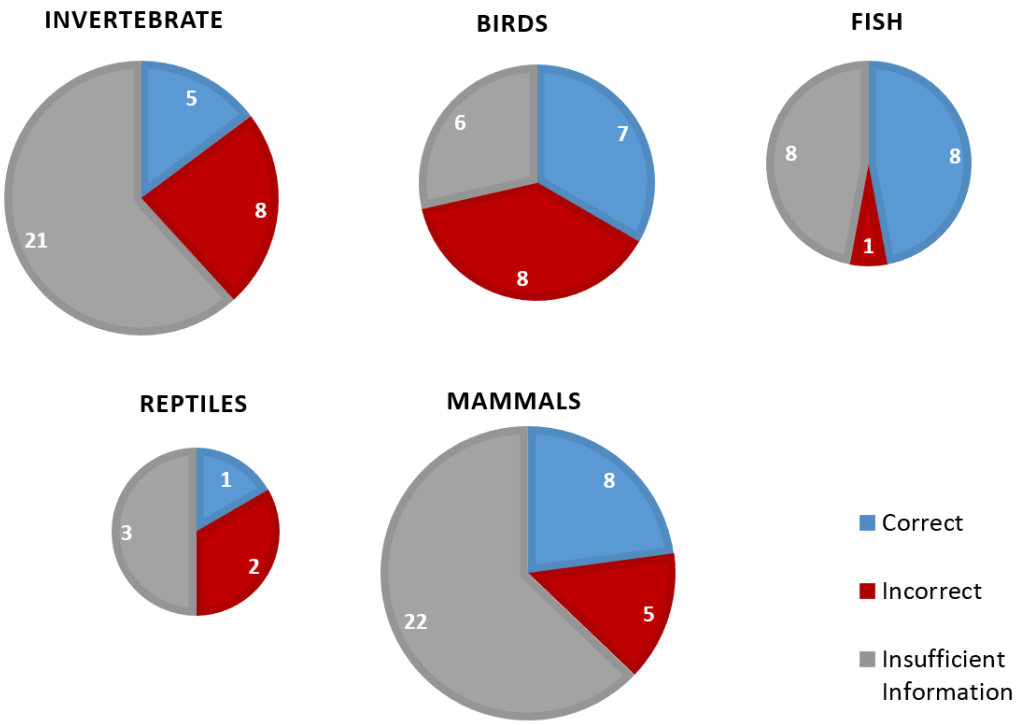
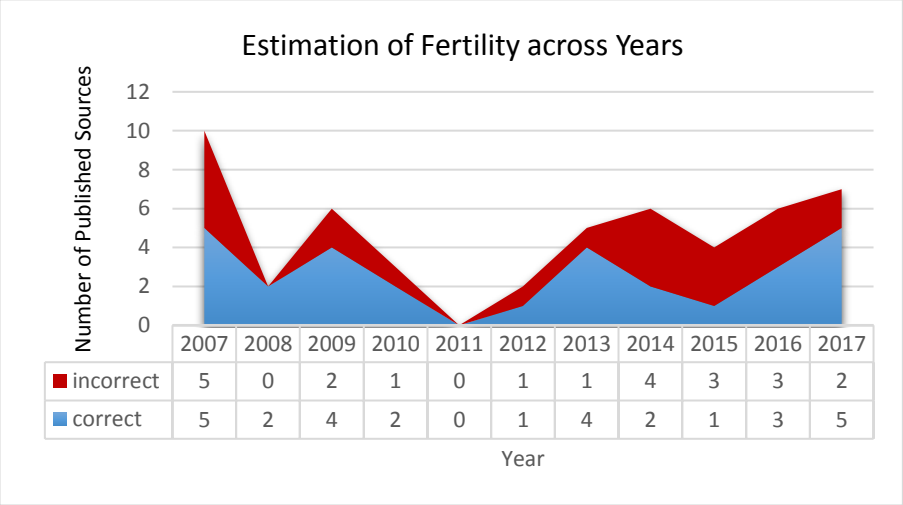


Figure 5. Pie charts representing number of papers obtained from each Taxa group that had incorrect estimation of fertility (red), correct estimation (blue), or insufficient information to assess fertility (gray). Size of pie chart reflects the relative number of papers for the corresponding taxa.

The number and proportion of papers that were marked as correct and incorrect estimation of fertility coefficient are shown in Figure 6. The number of papers reviewed varied between these years. The proportion of incorrect papers per year had no detectable trend ($P = 0.25$). This indicated that although there was no increase in mistakes over the years, there was also no foreseeable decrease.



	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
incorrect	5	0	2	1	0	1	1	4	3	3	2
correct	5	2	4	2	0	1	4	2	1	3	5

Figure 6. Stacked area graph of incorrect and correct fertility estimation between the year 2007-2017

The journal impact factor for the year 2017 is tabulated in Table 6 for journals corresponding to papers marked with incorrect fertility coefficient using InCites Journal Citation Reports (Clarivate Analytics, 2019). In the InCites Journal Citation Reports database, 160 journals were under the category labeled "Ecology" and ranked by impact factor. The median impact factor was 2.015, and the aggregate impact factor was 3.281. Not all journals found under the literature review were ranked under the ecology category in this database.

Table 6. List of journals corresponding to published papers used and the journal impact factor for year 2017. Boxed section corresponds to journals that published papers used in this sample without mistakes in fertility estimation.

Journal	Frequency	Wrong frequency	Journal Impact Factor	Rank in Ecology Category
Aquaculture	1	1	2.71	
Biological Conservation	1	1	4.661	20
Chelonian Conservation and Biology	1	1	0.828	
Ecological Modelling	3	1	2.507	60
Ecology	2	1	4.617	21
Endangered Species Research	1	1	2.312	
Environmental Toxicology and Chemistry	1	1	2.491	
Fisheries Research	1	1	1.874	
Functional Ecology	2	1	5.491	14
Human and Ecological Risk Assessment: An International Journal	1	1	1.508	
Journal of Animal Ecology	1	1	4.459	24
Journal of Applied Ecology	2	1	5.742	13
Journal of Avian Biology	1	1	2.488	
Journal of Mammalogy	2	1	2.139	
Journal of Wildlife Management	5	2	2.055	79
Natural Resource Modeling	1	1	0.875	
Neotropical Entomology	1	1	0.886	
PLOS One	3	2	2.766	
Population Ecology	4	1	1.644	
Restoration Ecology	1	1	2.544	58
Canadian Journal of Fisheries and Aquatic Sciences	1	0	2.631	
Conservation Biology	1	0	5.89	12
Ecological Monographs	1	0	7.828	7
Ibis	1	0	2.234	
Journal of Mathematical Biology	1	0	1.786	
Marine and Freshwater Research	1	0	1.674	
Marine Ecology Progress Series	1	0	2.276	72
Mathematical Biosciences & Engineering	2	0	1.23	
Molecular Ecology	1	0	6.131	10
Reviews in Fish Biology and Fisheries	1	0	3.299	
Scientific Reports	2	0	4.122	

3.2 Results for Alligator Matrix Population Model

The matrices constructed based on the descriptions in the paper resulted with a lambda of 0.87 for the northern population and 1.02 for the southern population, consistent with the values reported in the paper, with one modification that the duration in the subadult stage of the southern population was reduced to 3 years instead of 4 years. With this modification, both matrices also gave almost the same reproductive values and stable stage distributions listed in the paper.

For the northern population, the asymptotic population growth showed a small decrease when using model AN2, which incorporated the survival rate into fertility rate of adult and subadult stage in a four-stage model (Fig. 7). However, when juvenile transition rates were calculated using the asymptotic age-within-stage structure model in addition to corrections in AN2, the population growth rate increased. The largest population growth rate was achieved with AN4, an age-structured model without the inclusion of survival of adults in the fertility coefficient. When survival was included into the fertility coefficient in the age-structured models AN5 and AN6, the population growth rate decreased. The population growth rate for the age-structured models were all higher than the original stage-structured model. Additionally, the stage-structured model AN3 resulted in an estimation of lambda that was closer to that estimated with the age-structured models that included survival in the fertility coefficient. The asymptotic population growth for the southern population showed a small increase when survival rate was implemented into the fertility coefficient in the stage-structured models AS2 and AS3. The age-structured model without survival of adults in the fertility coefficient (AS4) had the highest

population growth rate among all models. When the survival rate was included in the age-structured models AS5 and AS6, the population growth rate decreased with AS5 having the smallest lambda. Additionally, the stage-structured model AS3 had an estimation of lambda closest to the age-structured model AS6.

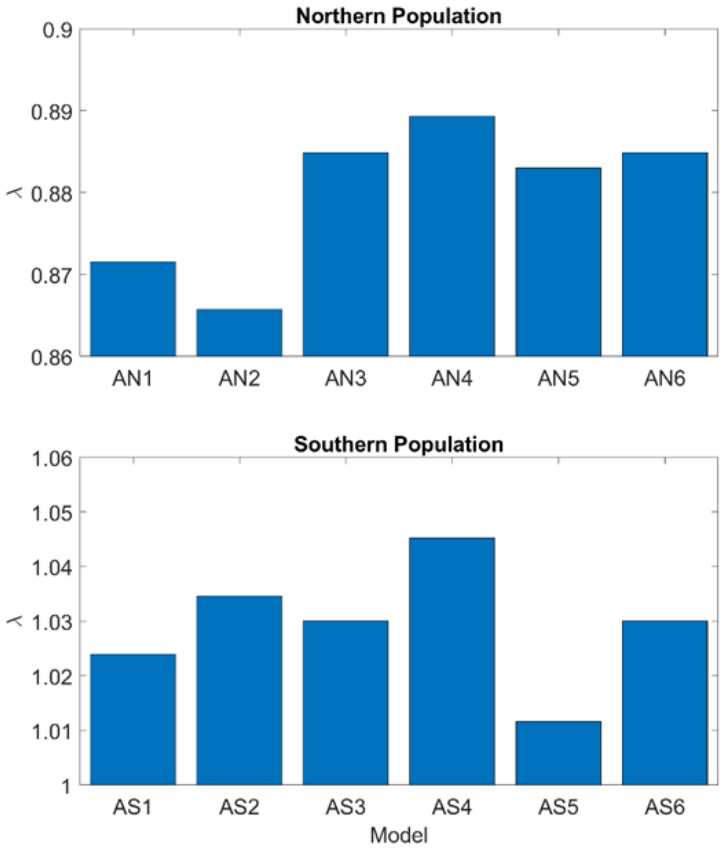


Figure 7. Asymptotic population growth rates of populations under AN1-AN6 and AS1-AS6 models. Reprinted with permission from Kendall et al. (2019).

When looking at the stable stage distribution (Fig. 8), there was a notable increase in the distribution of hatchlings and juvenile stages among models in the southern population (AS2 and AS3) when the survival rate was included compared to the original model. The northern

population had a more subtle increase among these stages. These increases came from the fact that the original matrices contain an extra egg stage. For the reproductive value (Fig. 9), stage-structured models had lower reproductive values for juveniles and subadults than the age-structured models in both northern and southern populations. Adult reproductive values were higher for stage-structured models than age-structured models in the northern population with the exception of model AN3 which had a similar reproductive value to those of age-structured models.

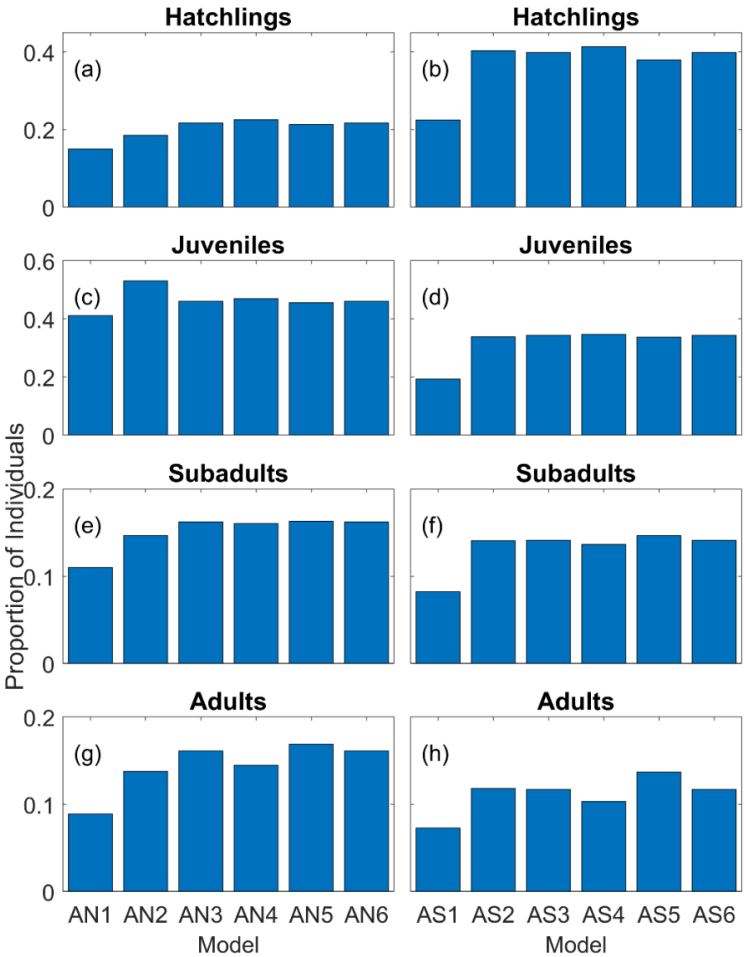


Figure 8. Stable stage distribution of hatchling, juvenile, subadult, and adult stages under the six different models. The panels on the left are for northern population, and the panels on the right are for southern populations. Reprinted with permission from Kendall et al. (2019).

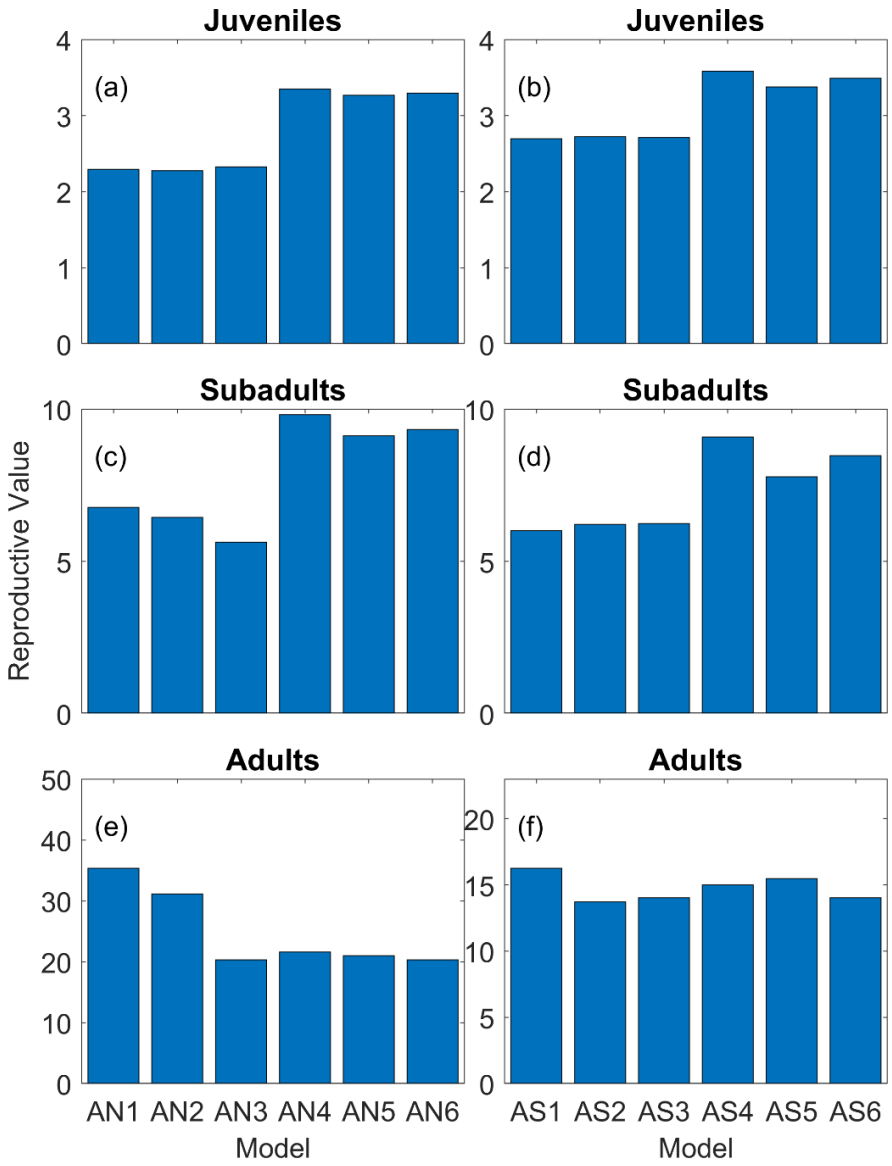


Figure 9. Reproductive value of juveniles, subadults and adults under the six different models. The panels on the left are for northern population, and the panels on the right are for southern populations. Reprinted with permission from Kendall et al. (2019).

Changes in sensitivity of lambda to stages were subtle (Fig. 10), with a small decrease in adult-stage seen in models AN3-AN6 from the original model. The sensitivity of lambda to the adult stage had a more distinguished decrease in model AS4 from the original model in comparison to other southern population models. When survival rate was included in the age-structured models, the sensitivity of lambda to the adult stage increased for the southern population. Similarly, changes in the elasticity of lambda to stages were also subtle, with elasticity of lambda to adult stage in stage-structured models being slightly higher than in age-structured models in the northern population. The elasticity of lambda to changes in the adult stage increased for the southern population when the survival rate was included in models AS5 and AS6 when compared to model AS4 (Fig.11).

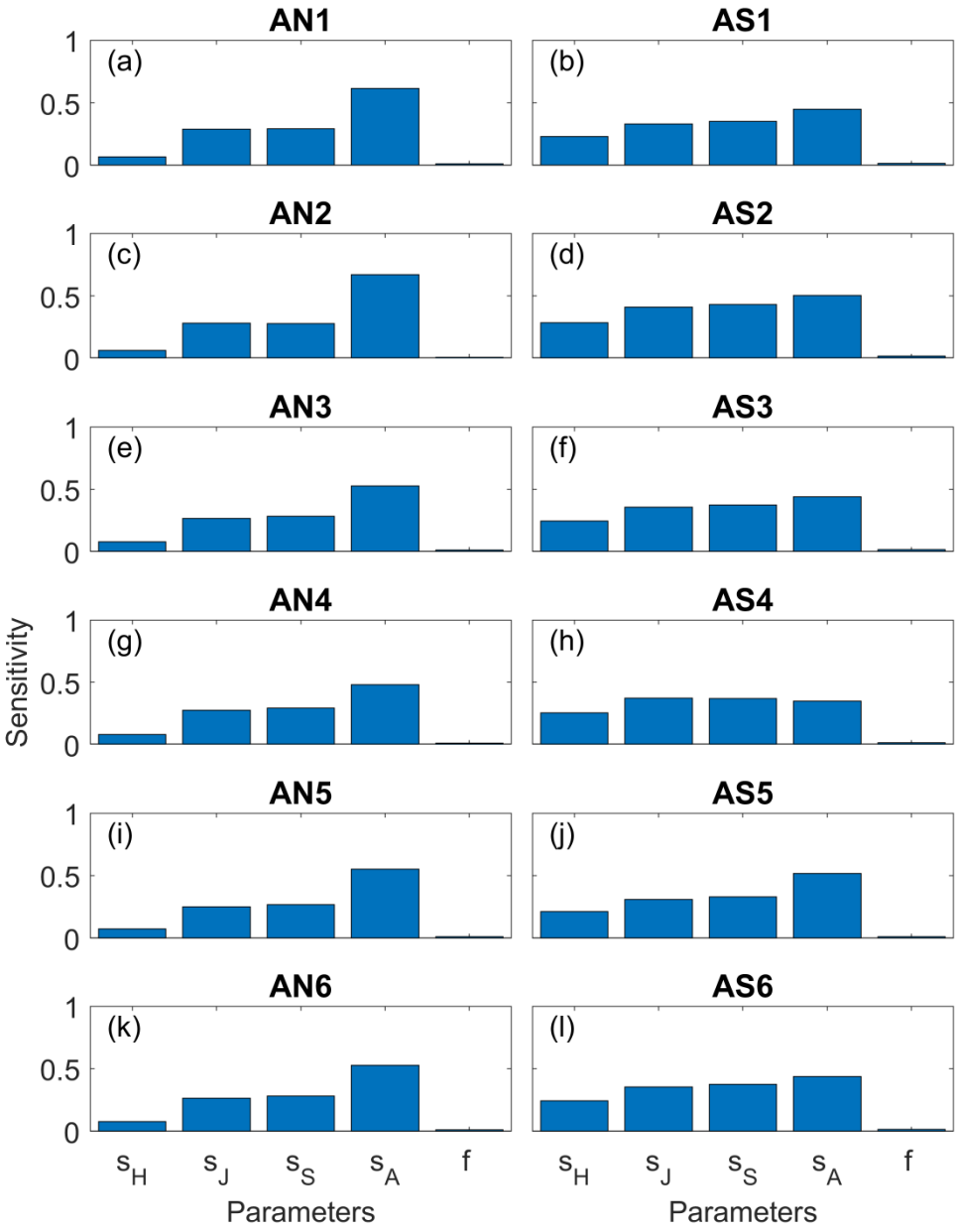


Figure 10. Sensitivity of lambda to stage-specific survival and fecundity. H: hatchling, J: juvenile, S: subadults, A: adults. The panels on the left are for northern population, and the panels on the right are for southern populations. Reprinted with permission from Kendall et al. (2019).

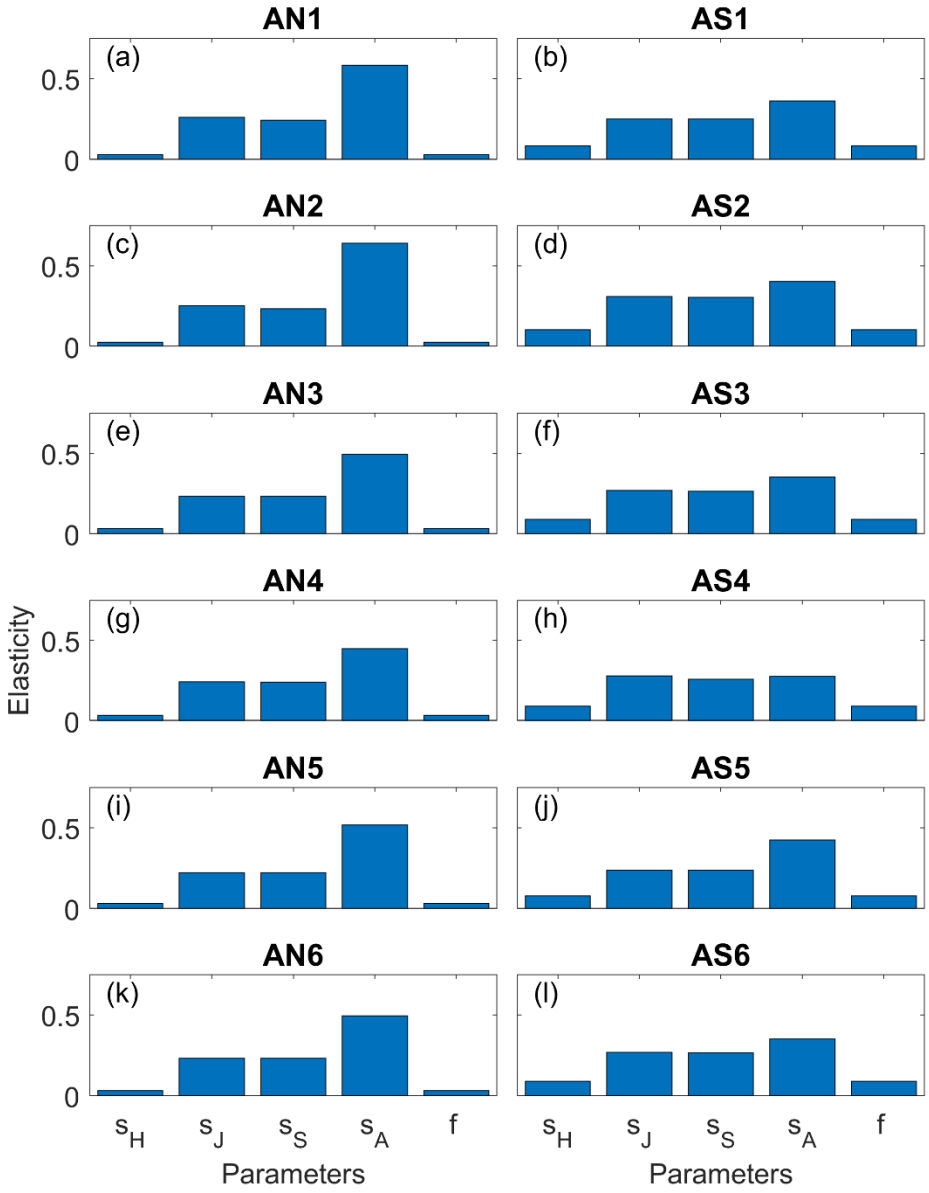


Figure 11. Elasticity of lambda to stage-specific survival and fecundity. H: hatchling, J: juvenile, S: subadults, A: adults. The panels on the left are for northern population, and the panels on the right are for southern populations. Reprinted with permission from Kendall et al. (2019).

The damping ratio appeared similar among all models for the northern population, stage-structured models had a damping ratio slightly higher than age-structured models. However, the

damping ratio for the southern population showed an increase for stage-structured models that included survival in the fertility coefficient AS2 and AS3, when compared to the original stage-structured models (Fig. 12). Damping ratio among the age-structured models remained similar after incorporating survival rate for both northern and southern populations.

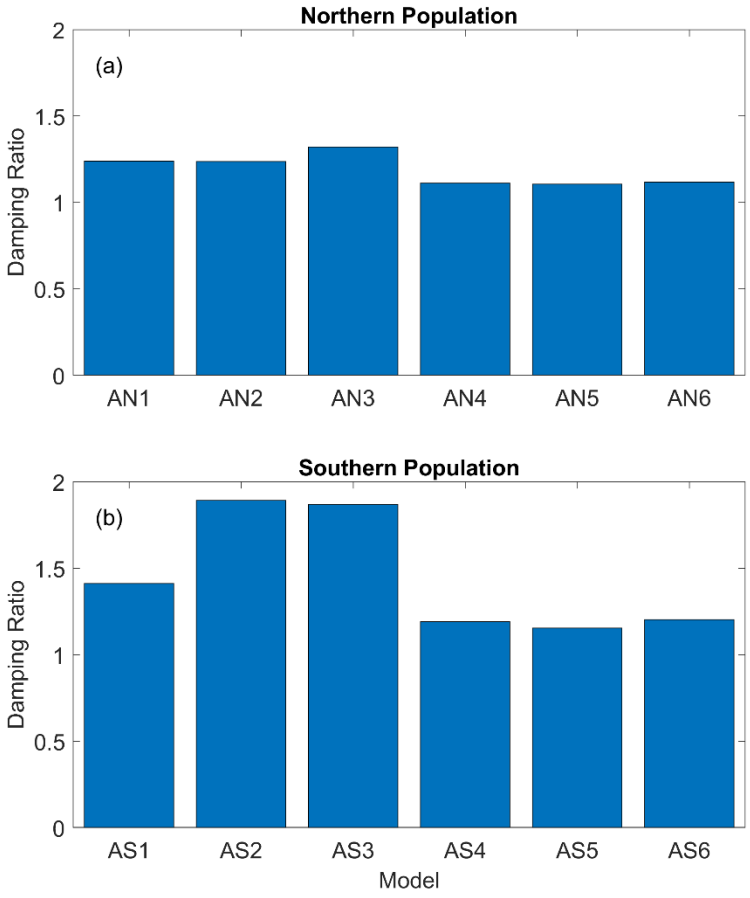


Figure 12. Damping ratio of populations under six different models. (a) Northern population and (b) Southern population. Reprinted with permission from Kendall et al. (2019).

Generation time for the northern population increased slightly when using model AN2 but decreased with model AN3 which used asymptotic age-within-stage structured

transition rates (Fig.13). The age-structured models with survival rate incorporated in fertility (AN5 and AN6) showed a decrease in generation time when compared to AN4. The stage-structured model AN3 had a closer generation time to the age-structured models that also incorporated survival rate into the fertility coefficient (AN5 and AN6). The shortest generation time was obtained with model AN2 and the longest generation time was obtained with AN4. The southern population showed an increase in generation time when stage-structured models incorporated survival (AS2 and AS3). For the age-structured models, generation time decreased when survival rate was used in models AS5 and AS6. The shortest generation time was obtained with AS4, while the longest generation time was generated by AS5.

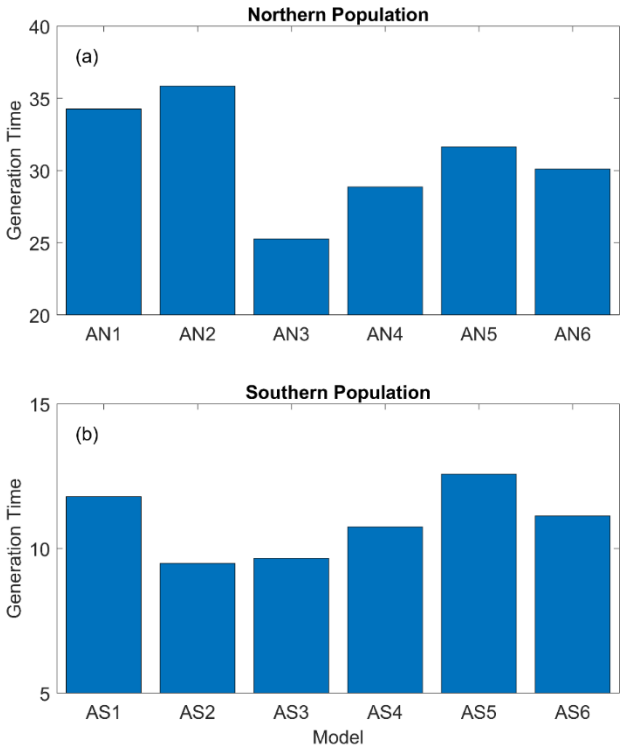


Figure 13. Generation time of populations under six different models. (a) Northern population and (b) Southern population. Reprinted with permission from Kendall et al. (2019).

4. DISCUSSION

4.1 Literature Review

4.1.1 Life History Strategies

The literature review provided insight into how well matrix population models were constructed in ecology. The results indicated there were common challenges when constructing population matrices for invertebrates and birds. Such challenges could also be associated with life history strategies of the organisms. Organisms with high fecundity and short generation time are seemingly difficult to survey in the field environment, and implementing them into a model may present further challenges. Assigning life histories to organisms presented among the reviewed papers helped confirm the speculation that some life history attributes may prompt errors in the application of matrix population models. However, it is important to note these life histories were crudely assigned considering the variety of species present in the reviewed papers. The methods for determining life history strategies used in this process were in no way as elaborate as the methods in Winemiller & Rose (1992). When assigning life history strategies, a unit of measure that was difficult to establish was generation time. Although generation time could be calculated using a population matrix, studies seldomly reported it or the entirety of the rates implemented into the models. Notably, calculating generation time using stage-structured models (the majority of these papers) have been shown to be inconsistent with true values (Lebreton, 2005). This inconsistency can result from the incorrect assumption of homogeneity among individuals within a stage in stage-structured models when in reality organisms with complex life histories could further be sub-divided into sub-stages (Fujiwara & Diaz-Lopez, 2017). For example, as fecundity declines with age in many organisms, younger individuals have

a larger expected contribution to the reproductive output of a population (Fujiwara & Diaz-Lopez, 2017); however, stage-structured models assume they contribute equally.

4.1.2 Common Mistakes & Alligator Matrix

When assessing each paper individually, the majority of mistakes in the estimation of fertility rate resulted from failure to include survival rate. As previously mentioned, without the inclusion of survival rate into the fertility rate, there is a spurious assumption that all individuals will survive to contribute to the growth of a population. The effect of this mistake is seen in the inflation of λ. This mistake could be attributed to the different terminology seen across literature. Among the studies reviewed, four different terms were used to define the parameter used in the first row of the population matrix, referred to in this study as fertility. These words included fecundity, fertility, maternity function, and pregnancy rate. Although all papers referenced Caswell's *Matrix Population Models*, the terminology used still varied among papers. A possible explanation for this could be that nonmodellers are redefining modeling terms to match to their own understanding of ecological notions (Kendall et al., 2019). This tendency could also explain why fecundity and fertility are the most commonly used terms to define fertility rate (as defined in this study) even though they have different meanings in terms of modeling. Among the reviewed literature there were instances in which fecundity was used to describe the fertility rate parameter in the matrix and as a result only included the number of offspring at birth produced without accounting for the survival of offspring over the duration of time unit. The fact that both terms begin with the same letter "*F*" often results in the notation for them being the same. This may make it difficult for novices to distinguish the notation "*F"* used in the literature. This may also be an explanation for the unintentional omission of survival.

Adjusting for survival rates between different reproductive stages also allowed room for error. Modeling the survival for stages with a shorter duration than the time-step of the model presented challenges in some studies. This was seen more often across organisms with egg stages. For example, Botteon et al. (2017) defined the fertility coefficient used in the matrix as "fecundity", and measured it as mean number of eggs per females. This probably resulted in papers categorized under the invertebrate and bird taxa group exhibiting higher percentages of mistakes. Census taken soon after breeding (post-breeding census) often account for the viability of eggs by including the egg survival in the fertility rate. However, short egg stage becomes problematic when the survival rate is implemented into the fertility coefficient that happens to span longer than the egg stage duration. An example of this was seen in the construction of two matrices for the northern and southern population of American Alligators by Dunham et al. (2014), where the egg stage was included in the stage-structured model. In this example, the egg stage is a quarter of the duration for the time step of the model; therefore, the fertility rate should have included adult survival rate prior to the release of the egg and egg survival rate during the time step. However, survival rate of adult was not included in the fertility rate. This example also referred to the fertility rate as fecundity and coincidently failed to account for survival. Omitting survival from the fertility coefficient in age structured models showed an overestimation (Fig. 7). The effect on lambda was slightly higher for the southern population which result from greater sensitivity of λ to fertility rate for the southern population than the northern population. However, the effects seen in lambda and the other demographic statistics were not drastic for these populations. Although the egg survival rate was slightly low (0.58/year), the adult survival, which represented nine out of twelve months of the survival rate, was relatively high (0.83/year).

A more significant effect on demographic statistics could be observed when/if a smaller survival rate (i.e., <<1) was omitted.

Birth-pulse populations were more common than birth-flow populations among the models reviewed. The birth-pulse population models included both pre-breeding and post-breeding census models. Estimating fertility for pre-breeding and post-breeding census differ in the types of survival rate used in estimating fertility rate with post-breeding census including the survival of offspring over a time step and pre-breeding including adult survival. The difference also results in the difference in the youngest age class used in the matrix population model. Structuring a model according to a post-breeding census may seem more appropriate when collecting vital rates for newborn stages but if age-specific or stage-specific birth rates and survival rates are present, a pre-breeding model can also be constructed from the data collected in a post-breeding census. Additionally, when dealing with stage-structured post-breeding models, fertility includes transition probabilities between stages. On the other hand, structuring pre-breeding stage-structured models does not require dealing with this additional complexity (Kendall et al., 2019). Kendall et al. (2019) recommends the model be constructed using the pre-breeding framework to reduce the likelihood of missing a survival term in the fertility coefficient and to eliminate fertility coefficients associated with transitions from non-reproductive to reproductive stages.

4.1.3 Journal Impact Factor

Overall the diversity in journal articles varied widely, with the 51 studies among 32 journals. The distribution of journals was uneven and sample size for each journal was small for comparisons between journals. However, there were errors found in the fertility coefficient among journal articles that have a high impact factor in ecology. With a median impact factor of

2.015 and an aggregate impact factor of 3.281, papers published in journals with an impact factor well above both values such as Journal of Applied Ecology, Functional Ecology, Biological Conservation, Ecological Modelling, and Ecology are of concern as they may be influencing similar mistake in future studies (Clarivate Analytics, 2018). Papers with an incorrect fertility coefficient were published evenly among journals, without any specific journal largely contributing more to the number of papers with mistakes. This pattern indicates that correct methods for parameterizing vital rates within matrix population models are not widely known, and thus detecting possible errors may be out of a reviewers' control. This could also be a reason why, although new tools for utilizing matrix population models have emerged since their development, there is no indication that errors have become less prevalent. Similarly, Kendall et al. (2019) performed a logistic regression of errors in constructing matrix population models, including errors in fertility coefficients, against year of publications and found that the frequency of this type of error had no detectable trend over time with a p-value of 0.198. Unfortunately, mistakes found among literature in journals with a high impact factor may influence the propagation of these errors, and perhaps there is much ambiguity between common ecological terms and demographic parameters used in these matrix population models. For this reason, a set of descriptive methods on how to include survival rate in the fertility rate for birth-pulse models are supplied to reduce future mistakes.

4.2 Suggestions for Calculating Fertility Rate

4.2.1 Introduction

The method used for estimating fertility rate for matrix population models depends on the reproductive strategy of the animal of interest and timing of data collection. There are diverse reproductive strategies of animals in the nature, and different methods are employed for

collecting data. Consequently, there is no single general one-fits-all protocol for estimating fertility rate. The goal of this section is to describe methods for estimating fertility rate under several commonly encountered situations. For example, animals may experience seasonal or repeated reproduction often referred to as birth-pulse and birth-flow reproduction in matrix population models, respectively. During the literature review the majority of the assessed papers (72%) dealt with organisms exhibiting birth-pulse reproduction (more commonly, pre-breeding or post-breeding). Therefore, this section will focus on protocols for estimating fertility rate for birth pulse reproduction.

Protocols for estimating fertility rate are categorized based on the timing of the observation (data) relative to reproduction (i.e. observation of eggs or hatchlings if oviparous or newborn offspring if viviparous) and whether animals are oviparous or viviparous. A complicated part of estimating fertility rate is that the timing of observations for determining population abundance/density (i.e. population vectors) and the timing of observations for determining fertility may not coincide. In some cases, the timing of observations of parents reproducing and the timing of newborn offspring, both of which are needed for fecundity calculation, may also be different, resulting in a situation commonly known as "anonymous birth" in which an individual mother cannot be matched to observed offspring (Caswell 2001).

Suppose a population matrix projects a population vector from time t to t+1. Then, fertility is, in general, the product of the three quantities, the survival rate of parents, per-capita fecundity, and the survival rate of offspring occurring during one-time unit, assuming survival rate is the same for all individuals in stage i throughout the time interval. The unit of time is commonly one year, but it could be another time unit depending on organisms. The duration of time between each occurrence of life events and observations within the time interval will be

denoted as Δt_x, where x denotes the order of occurrence of events so that $\sum_{x=1}^{k+1} \Delta t_x = 1$, where k is the total number of events within a time interval. It is noted that under the two special cases in which observations were made immediately before reproduction (pre-breeding census) and immediately after reproduction (post-breeding census), one of the two survival rates (the survival rate and parents and survival rate of offspring, respectively) can be omitted because the other survival rate spans the entire duration between t and t+1.

Table 7 shows the notations used in this section. The survival rate is often assumed to be a unit-less quantity (i.e. proportion), but it actually has a time unit. In this study, it is assumed that the time unit for survival rate is consistent with that of t. For example, if t is in year, survival rate S_i is the proportion of individuals that survive over one year. This definition is used consistently even if the duration of a stage is shorter than one time unit.

It is important to note that fecundity is the number of offspring per parent (i.e. per-capita rate). However, in sexually reproducing species, fecundity is often expressed in terms of female offspring per female parent when the dynamics of female abundance represent the dynamics of the entire population; this assumption is termed as the female dominance assumption (Caswell, 2001). Hence, the population vector includes the number of females in a corresponding stage. If a population vector includes both females and males, the fecundity rate is the number of offspring, including both male and female offspring, per parent, including both male and female parents. There is also a possibility of building a two-sex models (Jenouvrier et al. 2010, Miller and Inouye 2011, Fujiwara and Zhou 2013). Under two sex models, the numbers of female and male offspring per-female parent need to be calculated separately. For the purpose of this study, it is assumed that female offspring and the number of mothers are included in a single-sex

model. However, the examples shown below can be applied to the other cases by keeping track of females and males accordingly.

Table 7. Parameter and associated notations used.

Parameters	
m	The total number of female offspring at sample time
n	The total number of mothers at sample time
f_O	fecundity, the average number of female offspring per mother, determined at observation *O*
S_i	survival probability of individual at stage class i
F_j	fertility, product of fecundity and survival probabilities for type *j*
Other Notations	
R	The occurrence of the release of egg or individual from mother
H	The occurrence of egg(s) hatching
O	Observation of offspring during which time fertility is estimated
p	parent stage
e	egg stage
L	Larvae stage, stage after hatching or stage following release from mother

Note: $S_i^{\Delta t}$ *is equivalent to the fraction of time* Δt *over which stage i survives. Fractions of change in time t,* Δt*, for all stages within time interval must sum to 1.*

4.2.2 Field Observations of Oviparous Individuals

The following figures (Figures 14-17) are used to illustrate events during a time interval between *t* and *t*+1. Where R is the event in which eggs are released from mother, and *H* is the event in which the eggs hatch. Figure 14 illustrates a scenario where offspring of an oviparous population is observed (*O*) sometime (Δt_3) after egg has hatched. Fertility can be estimated in one of two ways depending on whether the number of mothers was also determined simultaneously with offspring or not. If the sampling for number of mothers takes place at the same time as the observation of offspring *O* (n_O), then F_1 will be the product of the average

number of offspring per mother at the observation of offspring *O* and the survival probabilities within the time interval.

$$F_1 = S_p^{\Delta t_1} S_p^{\Delta t_2} S_p^{\Delta t_3} f_O S_L^{\Delta t_4} \tag{1.1}$$

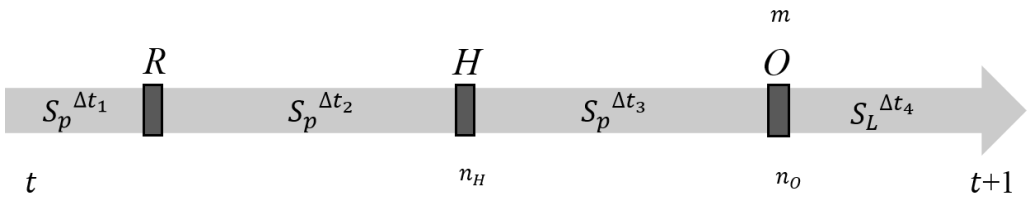


Figure 14. Timeline of occurrence, where observation and fertility estimation occurs at O after egg has been released (R) from mother and hatched (H).

where $f_O = \frac{m}{n_O}$. When $\Delta t_4 = 0$ the determination of fecundity and determination of population abundance (i.e. population vector) coincide.

However, if the sampling for the number of mothers takes place before the observation of offspring, differences in sampling time should be accounted for. For example, if it takes place very close to the time of hatching *H* (n_H), then F_2 will be the product of the survival rate of mothers until the time of observation (*O*), per-capita fecundity (f_O), and the survival of offspring until *t*+1. The per-capita fecundity at *O* is given by $f_O = \frac{m}{n_O} = \frac{m}{n_H S_p^{\Delta t_3}}$ because mothers will have to survive over Δt_3 from the observation to reproduce. Therefore,

$$\begin{aligned} F_2 &= S_p^{\Delta t_1} S_p^{\Delta t_2} S_p^{\Delta t_3} f_O S_L^{\Delta t_4} \\ &= S_p^{\Delta t_1} S_p^{\Delta t_2} S_p^{\Delta t_3} \frac{m}{n_H S_p^{\Delta t_3}} S_L^{\Delta t_4} \\ &= S_p^{\Delta t_1} S_p^{\Delta t_2} \frac{m}{n_H} S_L^{\Delta t_4}. \end{aligned} \tag{2.1}$$

**Note that $S_p^{\Delta t_3}$ in the numerator and denominator cancel each other. Then, the survival rates are multiplied so that the sum of all time durations on the exponents is 1 (i.e. $\sum_{x=1}^{k} \Delta t_x = 1$).

For an oviparous individual whose observation of offspring and mothers (*O*) occurs between release and hatching of eggs, as portrayed in Fig. 15, the survival of eggs (S_e) will need to be incorporated:

$$F_3 = S_p{}^{\Delta t_1} S_p{}^{\Delta t_2} f_O \, S_e{}^{\Delta t_3} S_L{}^{\Delta t_4} \tag{3.1}$$

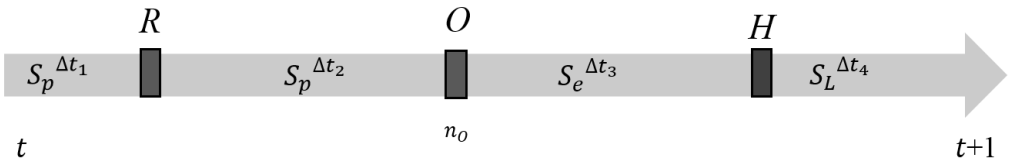


Figure 15. Timeline of occurrence, where observation and fertility estimation occur at O after egg has been released (R) from mother but before hatching (H). Here number of eggs observed is used to for number of offspring.

where $f_O = \frac{m}{n_O}$. Similar to the previous example, if the determinations of the number of eggs and parents are not simultaneous, the per-capita fecundity should be estimated after adjusting the number of mothers to the time of offspring (eggs) observation (*O*).

In the third scenario (Fig 16), the observation of offspring occurs before the release of eggs for oviparous organisms. This situation is common if the number of eggs within mothers is estimated (e.g. the number of eggs in the gonad of fish). Under this scenario, the survival of eggs (S_e) will also need to be incorporated:

$$F_4 = S_p^{\Delta t_1} f_O S_p^{\Delta t_2} S_e^{\Delta t_3} S_L^{\Delta t_4} . \quad (4.1)$$

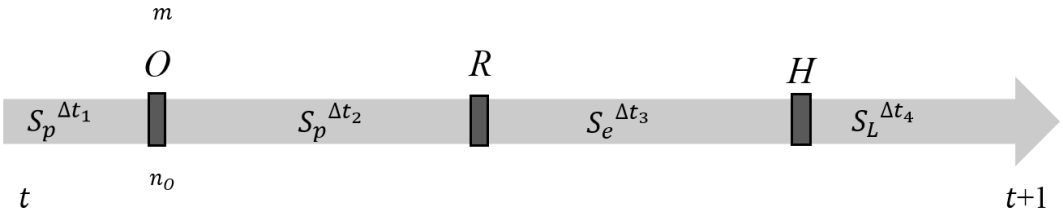


Figure 16. Timeline of occurrence, where observation and fertility estimation occur at O before egg has been released (R) from mother and hatched (H). Youngest individuals at time of occurrence O are approximately one time interval or breeding season old.

Fertility may also be estimated when the observation of offspring and mothers occurs near the beginning of breeding season, where the youngest offspring are at least as old as the length of one-time interval (Fig.17). This is common when offspring are not detectable for a long time. In this scenario, fecundity (f_{O+1}) is defined/estimated as the average number of offspring near the beginning of the time interval per female. To estimate for fertility at *t*, the mother must survive over time 1+ Δt_1 to breed. Then, the fertility over 1+ Δt_1 is

$$F_{5(+\Delta t_1)} = S_p S_p^{\Delta t_1} S_L^{\Delta t_1} f_{O+1}$$

Therefore, the fertility over one-time unit is

$$F_5 = S_p S_p^{\Delta t_1} f_{O_{t+1}} \frac{1}{S_L^{\Delta t_1}}, \quad (5.1)$$

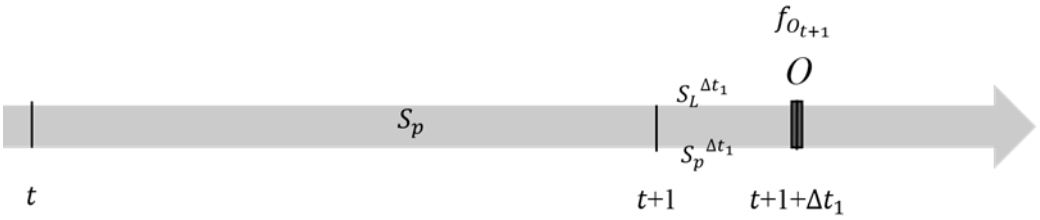


Figure 17. Time line where observation and fertility estimation occur at O, where offspring observed are at least as old as one time interval.

where $f_{O_{t+1}} = \frac{m_{t+1}}{n_{O_{t+1}}}$. The fecundity rate taken at this point includes offspring survival from t+1 to t+1+Δt with the rate $S_L^{\Delta t_1}$ as seen in Figure 17. The last fraction appears to revert the time unit of the fertility parameter to one time interval because the fecundity is estimated at time t+1+ Δt, instead of at t+1.

4.2.3 Field Observations of Viviparous & Ovoviviparous Individuals (live birth):

The life history and observational events for individuals that experience live birth (viviparous) or the release of individuals after hatching of eggs (ovoviviparous) are very similar to those used for oviparous organisms (Figures 14-17) except for the hatching of eggs outside of mothers (i.e. one less life history event). Therefore, *R* is the only life history event, in which an offspring is released from mother, and observation of offspring (*O*) can occur prior or after this event.

Fertility may be estimated when observations for determining fecundity occur relative to the release of offspring from the mother, before or after the event. In the former scenario as portrayed in Figure 18, fecundity is determined based on the reproductive state of mothers. Then, fertility should include: the survival probability of the parent stage from the start of the time

interval to the time of observation ($S_p^{\Delta t_1}$), survival probability from time of observation to time of release of offspring ($S_p^{\Delta t_2}$), fecundity (f_O), and survival probability of the newly born offspring for the remaining time interval ($S_p^{\Delta t_3}$):

$$F_t = S_p^{\Delta t_1} f_O S_p^{\Delta t_2} S_L^{\Delta t_3} \tag{6.1}$$

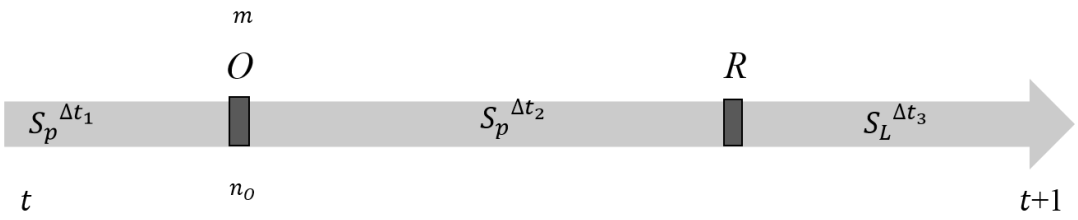


Figure 18. Timeline of occurrence, where observation and fertility estimation occur at O before release (R) from mother. Youngest individuals at time of occurrence O are approximately one time interval or breeding season old.

It is important to note that we are assuming the survival rate of offspring within mother is conditional on the survival of mother.

In the latter scenario as portrayed in Figure 19, fertility should include the survival probabilities of the parent before release of offspring ($S_p^{\Delta t_1}$), the survival probability of parents between release of offspring from mother and observation ($S_p^{\Delta t_1}$), the fecundity, and the survival probability of the offspring from the time of observation to the end of the time interval ($S_L^{\Delta t_3}$). This is because we are determining the fecundity based on the number of parents at $\Delta t_1+\Delta t_2$ so that parents must survive until this time.

$$F_t = S_p^{\Delta t_1} S_p^{\Delta t_2} f_O S_L^{\Delta t_3} \quad (7.1)$$

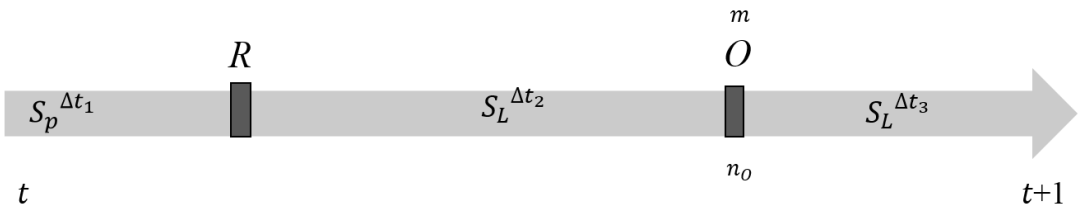


Figure 19. Timeline of occurrence, where observation and fertility estimation occur at O after release (R) from mother.

5. CONCLUSION

Matrix population models, like other research tools come with challenges. However, it is important to focus on how to overcome these challenges rather than discredit their entire findings. Although there are different types of errors one can make when calculating fertility, there appears to be a commonality among papers through the omission of survival rate for either offspring or adult. The occurrence of similar errors suggests there is enough ambiguity in the use of terms such as fecundity and fertility among literature that needs to be addressed, particularly when these errors affect asymptotic growth rate among other demographic measures. While these errors may not always affect λ at large magnitudes, the repercussions of an erroneous λ as an indicator of population status can result in misallocation of conservation efforts. This could result in that populations in need of more resources are not receiving them or populations in no dire need of assistance are receiving resources that would better benefit others. The uncertainty of these effects are enough to caution users and introduce approaches, as discussed in 4.2, to surmount persistent errors. Focusing on further development of tools in software already used by ecologist such as the mpmtools R package (Kendall, 2019) can help familiarize the use of matrix population models to a wider audience. Future development of tools should also aim to provide examples of probable mistakes and emphasize terms which have precise meaning among modelers. Often when presented with new subjects, getting acquainted with common mistakes can benefit beginning users.

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